





INDICATORS OF MOVEMENT USEFUL TO PROBLEMS OF  
BIOMASS ESTIMATION OF PELAGIC STOCKS

by

G.P. Bazigos  
FAO-Fishery Statistical Consultant  
Fishery Statistics Unit  
Policy and Planning Service

H.P. Henderson  
Senior Fishery Officer  
FAO-Fishery Resources Division

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**ABSTRACT**

Various indices are proposed for the study of movement in fish populations where the changes in spatial distribution of the population over time rather than the movements of individuals are of primary interest. The need for such indices arose in studying the precision and efficiency of acoustic surveys of the biomass of pelagic fish in Lake Tanganyika. Data from these surveys are used to illustrate the calculations and uses of the indices. Further, the need to measure and account for pattern and movement of fish in the design of catch assessment surveys and other fishery investigations is discussed. Finally, a general linear model of fish movement, tailored to the needs of statistical studies of the spatial distribution of pelagic fish, is suggested.



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## INDICATORS OF MOVEMENT USEFUL TO PROBLEMS OF BIOMASS ESTIMATION IN PELAGIC STOCKS

### 1. THE NATURE OF THE PROBLEM

#### 1.1 Introduction

Fish movement may be considered in terms of the behaviour of individuals, or the behaviour of groups such as shoals or even stocks. It may also be considered in terms of the behaviour of concentrations irrespective of the identity of the individual or groups that produce the concentrations. As a water wave moves without a net displacement of water particles, fish concentrations may move with only local movements of individual fish.

We do not suppose that the latter kind of fish movement is of any particular importance in explaining why changes in fish distribution take place or that such movement is a common feature of fish behaviour. We do wish to emphasize that unless individuals or groups can be made identifiable so that their individual position can be tracked over time, any movement observed must refer to the behaviour of concentration (or patterns) and not to the behaviour of individuals.

A fisherman is interested in knowing that there was a concentration of a particular kind of fish in one place and that the concentration has moved to another. It is of no importance whether or not both concentrations consist of the same individuals. In this paper we consider certain indicators of movement in this abstract sense which can be derived from data giving numbers or weights of fish in given areas, where these data show change over time and space.

Our consideration of movement was stimulated by problems arising from the statistical analysis of data obtained in acoustic estimation of the biomass of pelagic fish stocks showing large differences in the concentrations from place to place. Changes in the distribution of the fish both during and between surveys made it evident that movement was a factor that needed to be accounted for in the statistical analysis of these data.

Such methods of observation as acoustic sampling do not permit identification of individuals. Tracking of individuals is possible, from which a biological description of the movements within a population might be built up. However, a description suitable for improving estimators of biomass, and for studying a number of other fishery problems, may be obtained more simply by empirical methods.

#### 1.2 Position and movement

There are two aspects to the measurement of movement: position, and change or transition; a quantity of movement is regarded as the difference between two positions. In line with the discussion above, we may take the quantity  $\hat{Y}_i$  of fish within a particular area ( $\hat{A}_i$ ) as one position ( $P$ ). After a period of time, a new quantity  $\hat{Y}'_i = p'$  is observed in the same area. The difference  $(\hat{Y}'_i - \hat{Y}_i)$  may thus be regarded as measuring a movement of fish, although in the more usual sense it would be regarded as a change in concentration brought about by movement<sup>1/</sup>. Further, the concentration per unit area:

$$\hat{Y}_i/\hat{A}_i, \quad \hat{Y}'_i/\hat{A}_i$$

could also be regarded as positions, while their difference  $\hat{Y}'_i/\hat{A}_i - \hat{Y}_i/\hat{A}_i = \frac{\hat{Y}'_i - \hat{Y}_i}{\hat{A}_i}$  would then be a measure of movement based on concentration or density.

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<sup>1/</sup> Reproduction and death are alternative sources of change in concentrations

In situations where the total population may be regarded as closed, with movement occurring within a well defined space of area  $\hat{A}$ , it may be convenient to divide up the total space into regions (segments or strata) of areas,  $\hat{A}_i$  not necessarily equal such that  $\hat{A} = \sum \hat{A}_i$ .

If the population is closed, then the total quantity  $\hat{Y}$  ( $\hat{Y} = \sum \hat{Y}_i$ ) of fish in the whole area is always the sum of the quantities  $\hat{Y}_i$  over all regions, even though movement has taken place, that is even though the population has been redistributed.

Under these conditions it will also be convenient to measure movement in the above sense with respect to the fraction of the total population which would be expected in a particular region were the fish uniformly distributed in space. This amounts to defining a "position" relative to an average concentration rather than relative to a zero-concentration. Thus the difference between the observed quantity in a region and the quantity that would have been observed had the fish been uniformly distributed may be regarded as a position  $P_i$  of the  $i^{\text{th}}$  region:

$$P_i = \hat{Y}_i - \left(\frac{\hat{A}_i}{\hat{A}}\right) \hat{Y} = \hat{Y}_i - \hat{X}_i, \text{ where } \hat{X}_i = \left(\frac{\hat{A}_i}{\hat{A}}\right) \hat{Y}$$

$$P'_i = \hat{Y}'_i - \left(\frac{\hat{A}_i}{\hat{A}}\right) \hat{Y} = \hat{Y}'_i - \hat{X}_i$$

As before, the difference between two positions is regarded, in our sense, as movement.

$$\text{Movement} = P'_i - P_i = \hat{Y}'_i - \hat{Y}_i$$

### 1.3 The concept of patterns

If estimates of the quantity of fish are available for all the sub-regions of the total area of interest, the vector of the "positions" of the whole population given by:

$$\begin{array}{c|c} P_1 \\ P_2 \\ P_3 \\ \vdots \\ P_n \end{array} = \vec{P}$$

can be regarded as a description of the pattern of distribution<sup>1/</sup>. There are two general reasons for interest in pattern. Firstly, we are often concerned with the changes in pattern over time and with the problems of predicting such changes as natural events. Secondly, we are often concerned with the interaction of the pattern of fish distribution (or other distribution) with patterns of sampling, exploitation, or other such activities which can be altered both in intensity and pattern to achieve particular results.

The concepts of position and pattern are essentially static. In this paper emphasis is placed on establishing a proper framework upon which the dynamic concept of movement of fish populations without reference to individual identity can be developed.

<sup>1/</sup> Variation in the density of organisms from place to place, often observed through quadrat sampling, has been of special interest to plant ecologists - see: Kershaw, 1964; Patil, Pielou, Waters, 1971

#### 1.4 Problems of scale

The choice of the size of the sub-units or regions (strata) taken in constructing the above indicators of position, pattern and movement is often quite arbitrary. In general, different information is obtained by changing the size and/or position of the sub-units. The pattern vector  $\vec{P}$ , in other words, can be formed in many ways, its dimension is arbitrary.

In practice there is also difficulty in defining the total space occupied by the population. Real boundaries are often not very sharp.

The pelagic regions of oceans and large lakes may seem sufficiently uniform horizontally as to justify assuming that a particular fish is equally likely to be found in any portion of it, and hence that the expected value of the density in any region is the average density over the whole population space. In reality, however, there are many reasons for expecting substantial differences from place to place in fish distribution. These include gradients in physical conditions such as temperature and transparency, patterns of water currents which are established by the particular shape of the basin, time correlated factors, both physical and biological, which assure the distribution at a particular time is related to previous conditions and the previous distribution, and even direct interactions between individuals which lead to shoaling, spawning aggregation, or sometimes mutual exclusion.

The effects of such factors as suggested above tend to impose their own patterns upon the pattern of fish distribution. These patterns may be somewhat distinct owing both to differences in form of the pattern and to differences in the dimension or scale of pattern produced. If the sub-regions are chosen to be relatively small, the variation among regions and over time may be large owing to effects of shoaling, while if the sub-regions are large this variation may be large owing to the existence of major environmental differences within different parts of the pelagic region.

Thus an essential problem of studying the distributions of fish is that of adjusting the scale or dimensions of indices of position, pattern and movement so as to match the pattern characteristics of the processes under study.

## 2. THE PATTERN OF DISTRIBUTION OF PELAGIC FISH IN LAKE TANGANYIKA (ONE OCCASION)

#### 2.1 Estimated vectors

Using the results of the main echo survey of Lake Tanganyika<sup>1/</sup> (November 1973), estimates were calculated of the large-scale pattern of distribution of pelagic fish in the lake (one occasion). Specifically, for survey purposes, the lake was divided into five limnological zones (strata - see Figure 2.1.1), and estimates were calculated of the surveyed magnitude on a stratum basis. The Table below (Table 2.1.2) gives the estimated total fish biomass by stratum ( $\hat{Y}_i$ ) and the expected total fish biomass under an assumed uniform distribution ( $\bar{X}_i$ ).

Using the tabulated data (Table 2.1.2) we calculated the stratum sizes of the secondary magnitude  $D_i = \hat{Y}_i - \bar{X}_i$ , expressing the positions of the observed quantities of pelagic fish in relation to the expected quantities of fish. The vectors below, Vector-1 and Vector-2, give the estimated values of the secondary magnitudes  $\hat{D}_i$  and  $\bar{A}_i = \hat{D}_i/\bar{X}_i$  respectively:

<sup>1/</sup> K.A. Johannesson - Preliminary quantitative estimates of pelagic fish stocks in Lake Tanganyika by use of echo integration methods, EIFAC/74/I/Symp.54

G.P. Bazigos (1975) - The statistical efficiency of echo surveys with special reference to Lake Tanganyika, FAO, FIPS/T.139, 54 p.

## LAKE TANGANYIKA

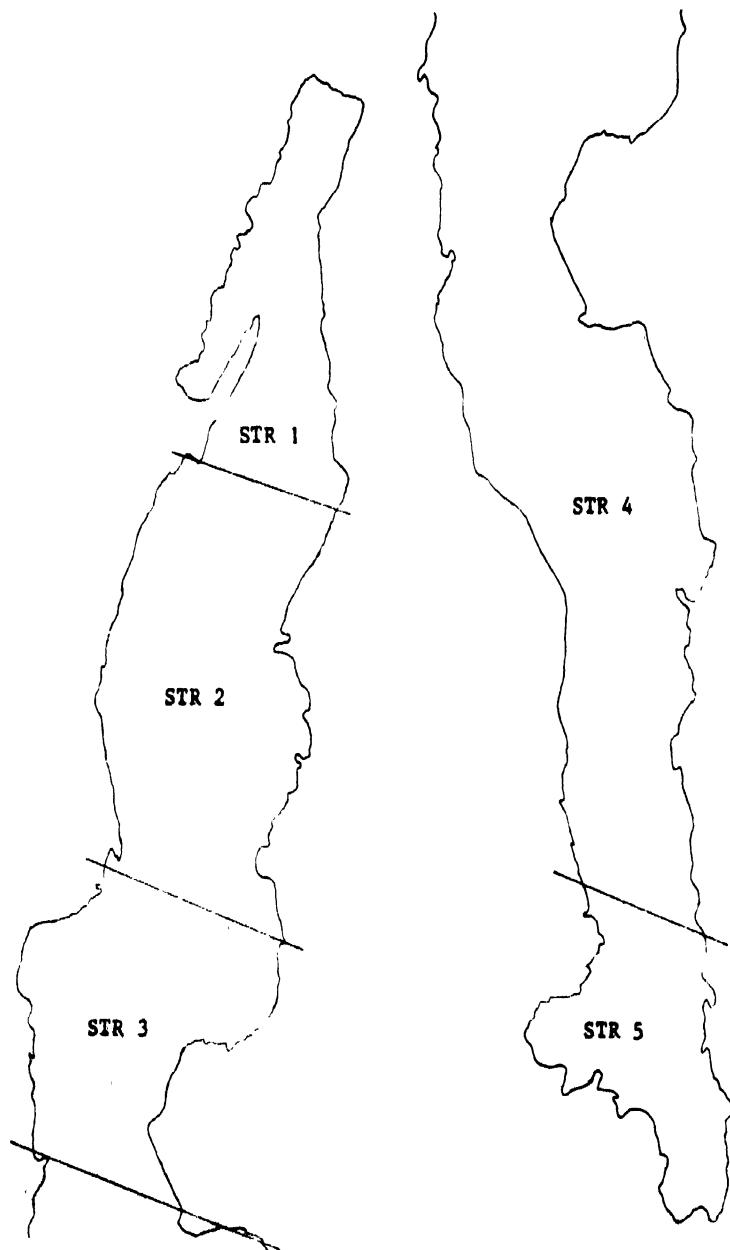


Figure 2.1.1 Area stratification

**Table 2.1.2      Estimated sizes of the magnitudes  $\hat{Y}_i$ ,  $\hat{x}_i$   
of Lake Tanganyika, November 1973**

Zones	Area		Estimated total biomass of pelagic fish* (t)	
	n mi <sup>2</sup>	%	$\hat{Y}_i$	$\hat{x}_i$
1. Burundi/ Cap Banza	698	10.81	88 686	329 916
2. Area near Kigoma	1 410	21.83	474 930	666 241
3. Area near Lagosa	1 121	17.36	434 101	529 819
4. Area near Kipili/Karema	2 446	37.88	2 015 940	1 156 080
5. Zambia	783	12.12	38 296	369 897
TOTAL:	6 458	100.00	3 051 953	3 051 953

\* Point estimates are based on the method of collapsed strata  
(for estimation purposes the night sample observations of  
the echo survey were used)

Vector-1 (tons)

$$\begin{bmatrix} \text{STR 1} & \hat{D}_1 = -241230 \\ \text{STR 2} & \hat{D}_2 = -191311 \\ \text{STR 3} & \hat{D}_3 = -95718 \\ \text{STR 4} & \hat{D}_4 = +859860 \\ \text{STR 5} & \hat{D}_5 = -331601 \end{bmatrix}$$

Vector-2 (%)

$$\begin{bmatrix} \text{STR 1} & \hat{\Delta}_1 = -73.12 \\ \text{STR 2} & \hat{\Delta}_2 = -28.71 \\ \text{STR 3} & \hat{\Delta}_3 = -18.07 \\ \text{STR 4} & \hat{\Delta}_4 = +74.38 \\ \text{STR 5} & \hat{\Delta}_5 = -89.65 \end{bmatrix}$$

It should be noted that the magnitudes which are involved in the calculations of  $\hat{D}_i$  and  $\hat{\Delta}_i$  are based on probability samples. In such a case the precision of  $\hat{D}_i$  and  $\hat{\Delta}_i$  can be calculated.

The calculated magnitudes show a concentration of fish in stratum 4 on both an absolute and a relative basis. If it could be established that this pattern was consistent over time the efficiency of future surveys could be improved by concentrating more of the sampling effort in stratum 4. It is known from previous analyses of these data that the variability of the individual observations from which the biomass is calculated increases in proportion to the biomass, and hence would be expected to be large in that stratum.

## 2.2 Estimated fish interchange curve

By using the data of Vector-2 we prepared the figure below (Figure 2.2.1). In this figure the estimated "fish interchange curve" gives an idea of the type of pattern of the distribution of pelagic fish in the lake during the survey period (November 1973). It is indicated that the highest level of localization of pelagic fish, herewith called the "centre of fish concentration", exists in Str.4, where the estimated total fish biomass in the stratum is about 75% higher than the expected volume of fish. The negative algebraic signs of the estimated percentages in Strata 1, 2, 3 and 5 show that the estimated total quantities of fish in these strata are lower than the expected volume of fish. Specifically, the rank order of the estimated negative percentages are: (a) Str.5 - with a value of about -90%; (b) Str.1 - with a value of about -75%; (c) Str.2 - with a value of about -30%; and (d) Str.3 - with a value of about -20%.

## 2.3 Estimated mathematical model

Another point which received consideration in our analysis is the effect of distance on the volume of fish between the individual positions on the one hand and the centre of fish concentration on the other hand. We divided the estimated biomass of pelagic fish ( $\hat{Y}_i$ ) by the expected biomass ( $\bar{X}_i$ ) to derive the ratio of the estimated to expected fish biomass volume, that is  $\hat{R}_i = \hat{Y}_i / \bar{X}_i$ . Also, we noted the distance  $d_{ii}'$ , which separates an individual stratum from the centre of fish concentration  $i'$  (Stratum 4). The table below (Table 2.3.1) gives the estimated magnitudes  $\hat{R}_i$ ,  $d_{ii}'$  and Figure 2.3.1 gives a graphical presentation of the existing relationship between the two magnitudes ( $\hat{R}_i$ ,  $d_{ii}'$ ).

**Table 2.3.1** Estimated total biomass ratios ( $\hat{R}_i$ ) within strata and distances ( $d_{ii}'$ ) between the individual strata and centre of fish concentration\*

Positions (Strata)	$\hat{R}_i = \hat{Y}_i / \bar{X}_i$ (%)	$d_{ii}'^{**}$ (km)	Remarks
STR 1	26.88	413	
STR 2	71.29	281	
STR 3	81.93	171	
STR 4	174.38	0	Centre of fish concentration
TOTAL:	100.00	-	

\* Data of Str.5 have not been taken into account in this analysis because of the low level of precision of the sample estimates

\*\* Expresses distances in km of the centre of an individual stratum from the centre of fish concentration

A visual assessment of the type of relationship portrayed in Figure 2.3.1 suggests a log of the ratio of empirical to expected biomass fish volume on the one hand and distance on the other. The estimated equation (method of least squares) is given by:

$$\hat{R}_i = a b^{d_{ii}'}$$

$$\text{or, } \log \hat{R}_i = \log a + (\log b) d_{ii}'$$

$$\text{or, } \log \hat{R}_i = 2.32004 - 0.00203 d_{ii}'$$

Figure 2.2.1 Estimated fish interchange curve,  
November 1973

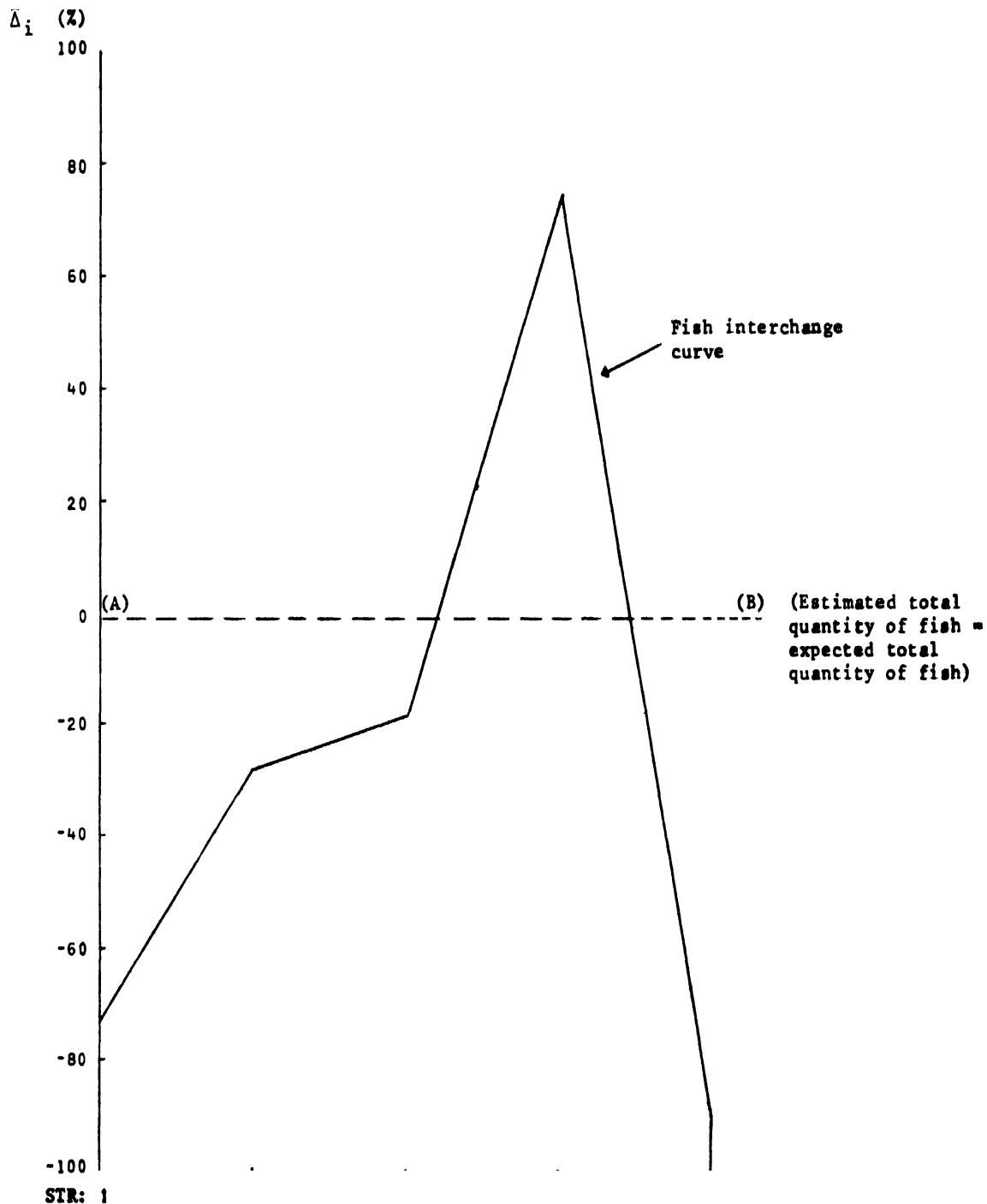
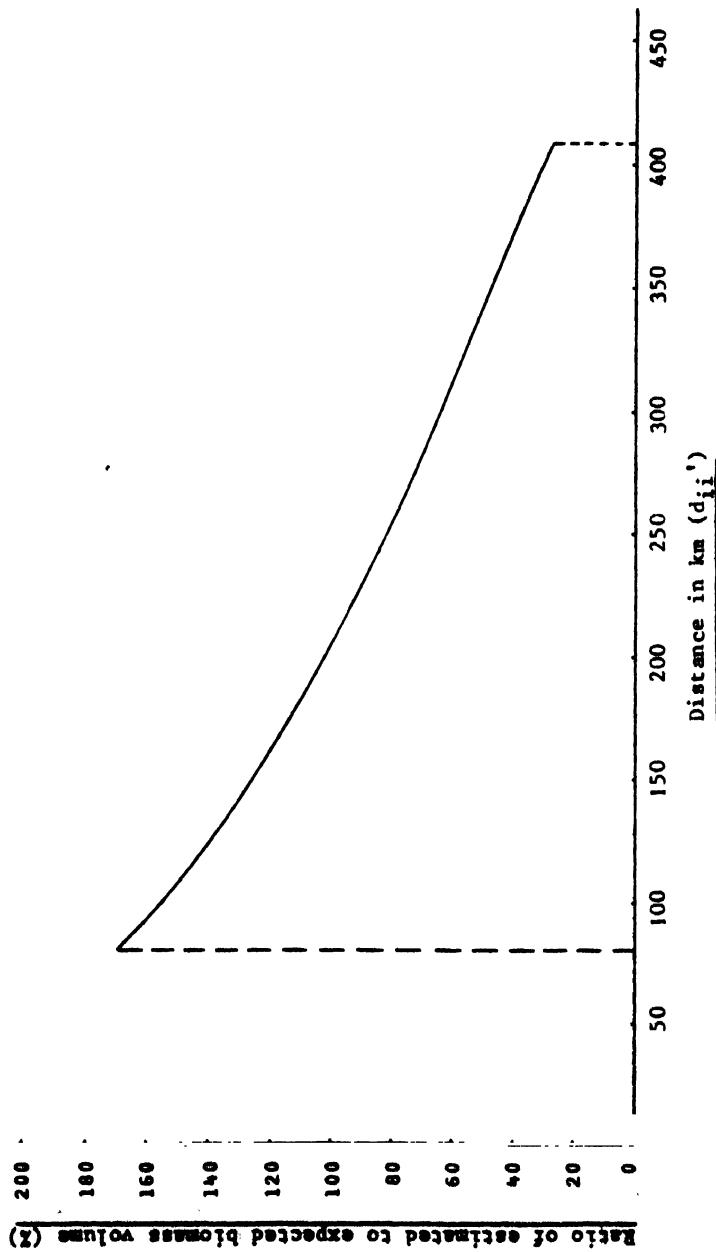


Figure 2.3.1  
Estimated trend curve of biomass ratios ( $\hat{R}_i$ ) within  
strata on distances ( $d_{ii'}$ ) of the individual stratum  
from the centre of fish concentration (STR 4),  
November 1973



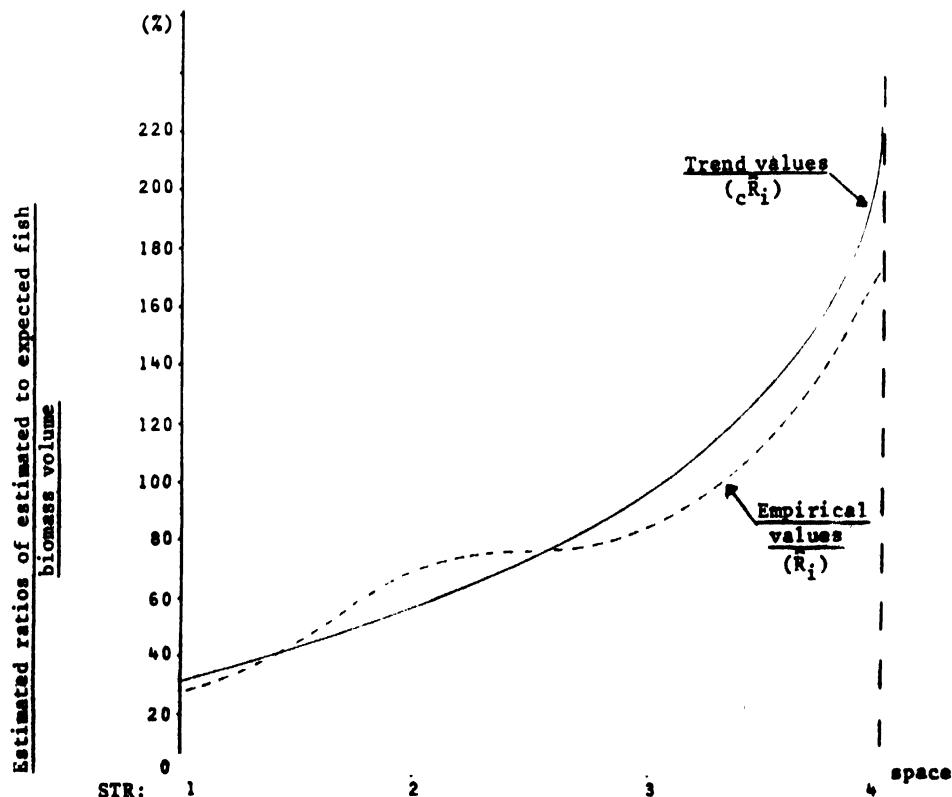
The table below (Table 2.3.2) gives the empirical and trend values of the sur-magnitude, and Figure 2.3.2 shows the estimated empirical and trend curves of estimated ratios.

Table 2.3.2 Estimated empirical values and trend values of the ratio of empirical to expected biomass volume of pelagic fish, November 1973

Positions (Strata)	Estimated ratios		$  \hat{R}_i - c\hat{R}_i  $ (%)
	Empirical values $\hat{R}_i$ (%)	Trend values $c\hat{R}_i$ (%)	
STR 1	26.88	30.31	3.43
STR 2	71.29	56.18	15.11
STR 3	81.93	93.95	12.02
STR 4	174.38	208.95	34.57

The established relationship ( $\log \hat{R}_i, d_i'$ ) depicts the interaction of fish in the individual stratum and the centre of fish concentration as a function of distance between them when the interaction is expressed in the level of localization of pelagic fish.

Figure 2.3.2 Estimated and trend curves of the estimated ratios of obtained to expected fish biomass volume, November 1973



### 3. ESTIMATED MOVEMENTS OF PELAGIC FISH OVER TIME (SUCCESSIVE OCCASIONS)

#### 3.1 The spatial pattern of centres of fish concentration

In the previous chapter the concept of centres of fish concentration (one occasion) was introduced. Over successive occasions, it is extremely important both theoretically and practically to find out whether the centre(s) of fish concentration are fixed or moving in the water body in which we are interested, as well as their strength over time. In a closed fish population the pattern of fish distribution over time is strongly affected by changes in the location in space of the centre(s) of fish concentration.

#### 3.2 Graphic presentation of fish movements

Graphic devices can be used to portray changes over time in the relation between empirical fish distributions and a uniform distribution. Graphic devices can also be used to show changes in the concentration of fish brought about by movements between two successive occasions.

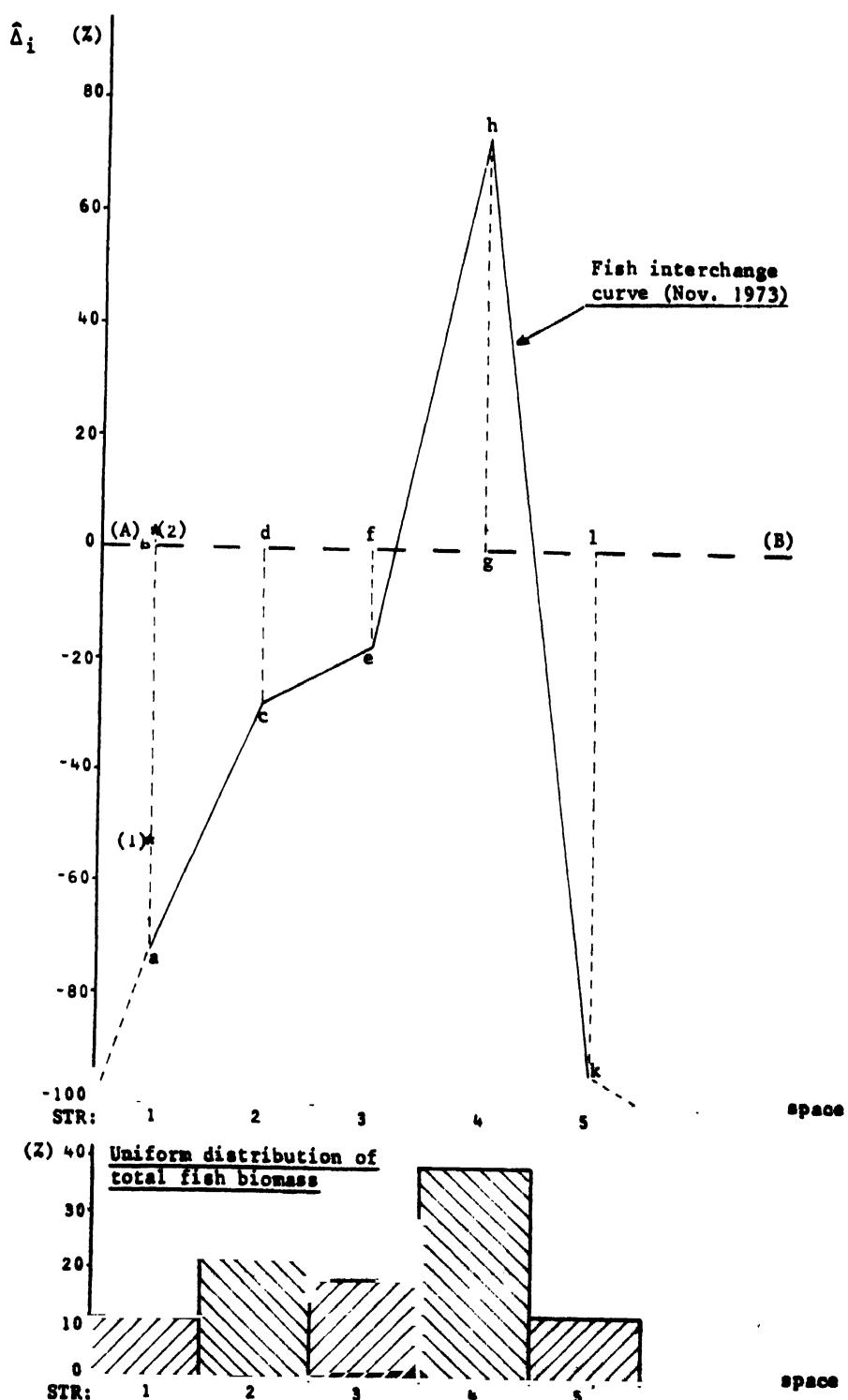
In the former case, vectors of type 2 (see Section 2.1) are calculated by making use of the results of the successive rounds of a current echo survey. The data are plotted on the same diagram and the respective "fish interchange curves" are drawn by round of the survey. Since the level of precision of the estimated ratios is relatively good for these acoustic surveys (data of Vector-2), the plotted curves based on the point estimates of the ratios can be considered as statistically reliable and facilitate a visual assessment of structural changes of the curves over time.

Specifically, changes over time in the relation of empirical fish distributions over a non-zero reference period can be portrayed on the diagram (see Figure 3.2.1 below) by marking the estimated ratio values of the successive rounds of the survey "on the distance line" connecting the ratios of the first round of the survey with the line AB. By making use of the results of the current echo survey, which covers only Str. I of the lake, we marked on the distance line ab (distance line of the previous main echo survey) the ratio values of two successive rounds of the current echo survey (Round 1: April 1974; Round 2: May 1974). As it is indicated in the diagram in Round 2 of the survey [\*<sup>(2)</sup>], the value of the estimated ratio was about equal to zero which in turn means that in May 1974 there was a heavy influx of fish in the stratum to the extent that the actual volume of fish biomass was equal to the expected quantity of pelagic fish<sup>1/</sup>. There was a small influx of fish to the stratum during the first round of the survey, and the actual fish biomass in April 1974 was about 52% lower than the expected one.

The fractile graphical method can be used to portray the level of movements of fish between two successive occasions of an echo survey. Specifically, the volume of fish biomass on a stratum basis of the one occasion of the survey is plotted on paper, and the successive points are joined by a line (curve). This constitutes the fractile graph of the one round of the echo survey. By using the same procedure we draw the fractile graph of the other round of the survey. The area lying between the two fractile graphs of the one and other round of the echo survey is defined as the "graphical distance". The shape and size of the graphical distance is used to portray changes in the level of concentration of fish over successive occasions of the survey brought about movement.

<sup>1/</sup> Assuming no change in the expected quantity as a result of net mortality or recruitment

Figure 3.2.1 Changes in the relation of the empirical distribution of pelagic fish over a non-zero reference period over time (STR 1)



### 3.3 Estimated indices of fish movements

In this section a first attempt is made to develop simple indices to measure changes in the level of concentration of pelagic fish over time. Specifically, two kinds of indices have been introduced:

- (a) Fish movement indices, type 1 ( $I^{(1)}$ ):  
The series of these indices are constructed to measure changes in the level of concentration of pelagic fish on a stratum basis over time.
- (b) Fish movement indices, type 2 ( $I^{(2)}$ ):  
These indices measure changes in an important property of the pattern of pelagic fish distribution over time (see Section 1.4).

#### 3.3.1 Fish movement indices, type 1

The magnitudes which are involved in the calculation of the indices of type 1 are estimates based on the results of successive echo surveys. If the estimated total biomass of pelagic fish in stratum  $i$  for two survey periods 1 and 0 are  $\hat{Y}_i$  and  $\hat{y}_i$  respectively, a simple measure of the relative movement of fish between the two survey periods is given by:

$${}_{1,0}I_i^{(1)} = \frac{|{}_{1,0}\hat{Y}_i - {}_{1,0}\hat{y}_i|}{({}_{1,0}\hat{Y}_i + {}_{1,0}\hat{y}_i)/2} \times 100 = \dots (\%)$$

$$\text{or, } {}_{1,0}I_i^{(1)} = \frac{|{}_{1,0}\hat{B}_i|}{{}_{1,0}\hat{C}_i} \times 100 = \dots (\%)$$

$$\text{where, } {}_{1,0}\hat{B}_i = {}_{1,0}\hat{Y}_i - {}_{1,0}\hat{y}_i \text{ and } {}_{1,0}\hat{C}_i = ({}_{1,0}\hat{Y}_i + {}_{1,0}\hat{y}_i)/2$$

If  $cv({}_{1,0}\hat{B}_i)$  and  $cv({}_{1,0}\hat{C}_i)$  are the estimated relative sampling errors of  ${}_{1,0}\hat{B}_i$  and  ${}_{1,0}\hat{C}_i$  respectively, an approximate formula for the estimated relative precision of  ${}_{1,0}I_i^{(1)}$  is given by:

$$cv({}_{1,0}I_i^{(1)}) = \sqrt{cv^2({}_{1,0}\hat{B}_i) + cv^2({}_{1,0}\hat{C}_i) - 2\bar{\rho} cv({}_{1,0}\hat{B}_i) cv({}_{1,0}\hat{C}_i)}$$

where,  $\bar{\rho}$  is the estimated linear correlation coefficient between  ${}_{1,0}\hat{B}_i$  and  ${}_{1,0}\hat{C}_i$ .

The index can be calculated either for a fixed base period or for moving base periods. In the latter case the estimated total biomass of pelagic fish in stratum  $i$  for each round of the survey is compared with the total fish biomass of the preceding round.

The table below (Table 3.3.1) gives the estimated total biomass of pelagic fish over time in Str.1 of Lake Tanganyikal<sup>1</sup> (see Chapter 2). The table also provides the estimated indices of fish movement based on a fixed base period (col.2) and a moving base period (col.3).

Table 3.3.1 Estimated total biomass of pelagic fish in Str.1 of Lake Tanganyika over time and estimated fish movement indices, type 1 (%)

Survey period	Estimated total biomass (t)	$I_i^{(1)}$	$\bar{I}_i^{(1)}$
		(Base period= April 1974)	(Moving base period)
	(1)	(2)	(3)
1974: April	159 000	0	0
May	339 000	72.29	72.29
July	181 000	12.94	60.77
September	178 000	11.28	1.67
November	171 000	7.27	4.01

An evaluation of the point estimates of  $I_i^{(1)}$  (col.2 of the above table) indicates that during the year 1974 (the only exception being May), the level of movements of pelagic fish in Str.1 of the lake should be considered as low with the values of  $I_i^{(1)}$  ranging from 7% to about 13%. In May 1974 there was a heavy influx of fish into the stratum and this is reflected in the estimated value of  $I_i^{(1)}$ . Considering the subsequent return to a low level, the tabulated values of also suggest that the influx in May resulted from immigration from other strata rather than recruitment of young stock, and that the probability of non-local stocks entering Str.1 of the lake within a year can be roughly estimated 0.20.

### 3.3.2 Fish movement indices, type 2

Fish movement indices, type 2 are estimated to measure changes in the pattern of fish distribution over time.  $I^{(2)}$  is constructed by aggregating the estimated values of  $I_i^{(1)}$ . Specifically, in order to allow each stratum to have the proper influence on the index, we constructed a weighted aggregated index:

$$I^{(2)} = \left( \frac{1}{\sum w_i} \sum w_i \cdot I_i^{(1)} \right) 100 = \dots (\%)$$

The sets of the estimated weights ( $w_i$ ) used in the above index express the relative importance of each stratum in terms of volume of biomass of pelagic fish. The values of  $w_i$  can be estimated either by considering the volume of fish biomass at the base period of the index, i.e.  $w_i = \frac{V_i}{\sum V_i} + \frac{\sum V_i - V_i}{\sum V_i}$ , or by considering the volume of biomass of pelagic fish under uniform distribution, i.e.  $w' = \frac{X_i}{\sum X_i} + \frac{\sum X_i - X_i}{\sum X_i}$ . A large value of this index will result from a large change in the distribution of biomass among strata between the two times (0.1) of observation.

#### 4. THE RELATIONSHIP BETWEEN THE SPATIAL DISTRIBUTION OF THE INTENSITIES OF FISH LOCATION AND OF FISHING, SAMPLING AND MARKING OPERATIONS

##### 4.1 Catch assessment surveys (CAS)

The output of a fishing industry within a given period of time may be defined as the catch resulting from fishing operations, or inputs, of the fishing economic units of the industry. Catch assessment surveys are designed to obtain estimates of the input items, i.e. fishing effort, and output items of a fishing industry over time. Further, trends of the secondary statistical magnitude catch per unit effort (CUE)<sup>1/</sup> are used in order to portray changes in the abundance of the respective harvestable stocks over time. Although the procedure of calculating the size and level of precision of CUE is rather simple - provided that reliable statistical data of the respective primary magnitudes are available - its statistical power as an indicator of stock density must be reviewed in the light of the viewpoint we have presented.

Only in the ideal situation in which the fishing effort and the exploited stocks are uniformly distributed in space is the estimated value of CUE a powerful indicator of stock density. The level of accuracy of the estimated magnitude CUE over time is a function of the level of concordance between the spatial pattern of centres of fish concentration on the one hand, and on the other, of the shape of pattern of the area of distribution of fishing effort. For example, if the fish concentrations are fixed over time and their locations are outside the vicinity of the active fishing boats, the calculated value of CUE provides a biased estimate (under-estimation) of stock density. On the other hand, if there is a high degree of localization of the active fishing boats around the fixed centre(s) of fish concentration, the estimated value of CUE provides an over-estimation of stock density. In the case of moving centres of fish concentration the level of accuracy of CUE over time depends on the level of concordance between the strength and location of fish concentration centres, and centres of concentration of fishing effort in space.

From the foregoing discussion, it is obvious that fluctuations of unadjusted CUE time series over time do not necessarily indicate parallel changes of the surveyed fish stocks. The existing relationship between the fish concentration centres and fishing must be studied before the results of such an operation can be predicted.

##### 4.2 Tagging or marking surveys

###### 4.2.1 The statistical efficiency of tagging surveys

Tagging surveys (or experiments) are often used to seek information on movements of fish. The basic design of such a survey is the release of a number of fish with marks or tags affixed (individual sample survey units) at one time in one or more originating areas, and to record the time and location ("terminating area") of subsequent recapture of any of these fish. For ease of discussion we refer to the compound event consisting of a release of an individual fish and subsequent recapture of the same fish as a "trip", whether the terminating area is different than, or the same as, the originating area. If there is a synchronous relationship between the movements in space of the fish biomass and of the trips taken by the selected (tagged) sample survey units on the other hand, the results of a tagging survey can be used to portray the mobility pattern of the fish biomass. To test for such synchrony, one needs the results of two parallel surveys, e.g. an echo survey of biomass distribution and a large-scale tagging survey.

<sup>1/</sup> For a given fishery, CUE is a secondary magnitude and is calculated as a ratio of two primary magnitudes, i.e. total fish catch and the effort involved to obtain the catch. Furthermore, estimators based on the ratio estimation can be developed in order to calculate the level of precision of the estimated magnitude - see: G.P. Bazigos, The design of Fisheries Statistical Surveys - Inland Waters, FIPS/T.133, 1974

It should be noted from what has gone before that the power, in a statistical sense, of such an experiment, will depend on the degree to which the distribution of the tagged sample units at the time of release reflects the distribution of biomass at the same time. It is also evident that the time of recapture of a particular fish cannot in practice be pre-determined<sup>1/</sup>. For this reason the effort expended in recapture should also be distributed as the population biomass for optimal results.

#### 4.2.2 The probability point of view

In order to relate the movement of individual fish to the movement of centres of fish concentration, we have adopted a point of view based on probability. If, from an efficient marking experiment, the relative frequencies of all possible trips taken by representative individuals is established, we are in a position to study the probabilities of specified movements and their relationship to population movement.

Assume that the surveyed area has been divided into  $k$  strata ( $i = 1, 2, 3 \dots k$ ) and that at time  $t_1$ , the total number of fish in the  $i$ th stratum is  $N_i$  ( $N = \sum_i N_i$  total size of the population). Further, suppose that  $M_i$  of these  $N_i$  are tagged distinctively with respect to stratum  $i$ . At time  $t_2$ , some of the  $M_i$  fish ( $m_{(i)i}'$ ) are recaptured in stratum  $i'$ . We then define a relative frequency  $f_{(i)i}'$ , or estimated probability  $\bar{P}_{(i)i}'$ ,

$$f_{(i)i}' = \bar{P}_{(i)i}' = \frac{m_{(i)i}'}{\sum_i m_{(i)i}'} = \frac{m_{(i)i}'}{m_{(i)}}$$

$$\text{where, } m_{(i)} = \sum_i m_{(i)i}'$$

with which a fish originating in stratum  $i$  is found in stratum  $i'$  after the time interval  $\Delta_t = t_2 - t_1$ . In our words,  $P_{(i)i}'$  is the probability that a fish will make a particular kind of trip in that interval, and all such probabilities estimated for the individual stratum and for the given time interval may be displayed as a probability matrix of dimension  $k$ .

It is of particular interest to determine the relationship of such experimentally determined probability matrices to a priori probabilities based on very simple expectations. Assume that the population is homogeneous as far as movements of individuals in space are concerned, and that the position in space of any particular fish at time  $t_2$  is independent of its position at time  $t_1$  for any interval  $\Delta_t = t_2 - t_1$ . Under these conditions we might expect that, for a fish in stratum  $i$  the probability of a journey terminating in stratum  $i'$  will be:

$$P_{ii}' = \frac{A_{i'}}{A}$$

$$\text{where, } A_{i'} = \text{area of terminating stratum.}$$

$A = \sum_i A_i$  = total area available for termination of the journey (total area available<sup>1/</sup> to the population).

<sup>1/</sup> Use of remote-sensing methods (sonic tags) is not considered here

Clearly, a model of the existing relationship of  $\hat{P}_{ii}'$  and  $\hat{P}_{ii}'$  expressed in relation to the distance separating  $i$  and  $i'$ , the length of the interval  $\Delta_t$ , seasonality of  $t_1$  (or  $t_2$ ) and other control variates, would be of value in describing the changes to be expected in the movements of the sample units of the survey and population. As  $P_{ii}$  and  $\hat{P}_{ii}'$  are defined upon movements of individuals, it remains to be shown by experiment that such movements are in fact synchronous with the movements of fish concentrations.

#### 4.3 A matrix model of fish movements

In Section 1.3 are defined the patterns of fish distribution in space as the position vector  $\hat{P}_t$  composed of indices representing concentration of biomass in each defined stratum  $i$  at a particular time  $t$ . We now pose a general problem of fish movement as it arises from the aforementioned problems of the study of pelagic fishing. Given the pattern of distribution of fish at time  $t_1$ , what, if anything can be said of the pattern of distribution at time  $t_2$ . In other words, we seek the relationship that predicts  $\hat{P}_{t_2}$  in terms of  $\hat{P}_{t_1}$  and such other factors as necessary and sufficient. In simplest form we may assume a linear matrix equation of the form:

$$\hat{P}_{t+1} = A \cdot \hat{P}_t$$

where  $A$  is a multiplicative  $k \times k$  matrix operator. If the elements of the matrix  $A$  are simple transition probabilities independent of  $\hat{P}_t$ , the model is known as a Markov chain.

The probability defined in Section 4.2.2 in relation to the marking experiment gives the probability that a fish in stratum  $i$  at time  $t_1$ , if recaptured at time  $t_2$  will be recaptured in stratum  $i'$ . It is also on the average, the fraction of the  $N_i$  fish in stratum  $i$  at time  $t_1$  that will be in stratum  $i'$  at time  $t_2$ , provided the marked fish do not behave differently than the rest of the population (assumption of homogeneity of individual survey unit), and there are no losses on the way. Therefore, we may write:

$$\hat{N}_{i'} = \hat{P}_{ii} \cdot N_i$$

where  $\hat{P}_{ii}'$  are the probabilities derived from the (complete) marking experiment. We may further note that if the process is Markovian over a defined interval as described above, an equilibrium distribution will be reached dependent only upon the probability matrix  $\hat{P}_{ii}'$ . Should  $\hat{P}_{ii}'$  be identical to the expected probabilities

$$\hat{P}_{ii}' = \frac{\hat{A}_{i'}}{\sum_j \hat{A}_{ij}} ,$$

then the equilibrium distribution will be the "expected" uniform distribution (Section 1.2).

## 5. SUMMARY

In order to facilitate the study of certain problems of estimation of characteristics of fish populations, we have discussed fish movement as a process of change in the spatial distribution of a population rather than as changes in the locations of individuals. The approach taken requires a division of the space inhabited (or inhabitable) by the population into sub-spaces, regions, or in the statistical sense, strata, within which the distribution of individuals is assumed to be homogeneous or with respect to the problem at hand, unimportant. Movement is considered as change (in biomass or biomass density) over a discrete interval of time. Based on this view, a number of indices could be defined expressing either the differences in biomass density among strata at a fixed time, or changes in the biomass density of particular strata over time. The former we associate with the term pattern and the latter with movement.

This way of thinking about pattern and movement corresponds to the usual statistical conceptualization of biomass estimation procedures and lends itself to a probabilistic treatment of fish movement. In a subsequent paper we intend to examine several sets of data describing successive position vectors of fish biomass and address the question of optimal design of sampling surveys for the populations from which the data were derived. In particular, the selection of a number of strata and an interval of time appropriate to specific problems and to the natural characteristics of the movements of the population will be discussed.

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